

GENERIC BOUNDARIES IN THE PODOCARPACEAE

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Synopsis

Generic boundaries in the Podocarpaceae are critically reviewed in the light of recent data on gametophyte development, embryogeny, cytology and vegetative anatomy. While there is general support for the smaller genera, both *Dacrydium* and *Podocarpus* appear to be artificial assemblages. It is concluded that *Dacrydium* should be divided into at least five genera, and that each of the eight sections of *Podocarpus* should be raised to generic rank.

INTRODUCTION

The Podocarpaceae is a family of conifers of mainly southern distribution, and includes seven genera. Five of these, viz. *Phyllocladus* L.C. and A. Rich., *Acmopyle* Pilger, *Microstrobos* Gard. and Johns. (*Pherosphaera*), *Microcachrys* Hook. f., and *Saxegothaea* Lindl., either comprise a small number of obviously closely related species, or are monotypic (Table 1). Both *Podocarpus* L'Herit. ex Pers. and *Dacrydium* Soland. ex G. Forst., however, include a much larger number of species which have been variously arranged into subgenera and sections.

The taxonomy of *Dacrydium* is in a very unsatisfactory state. Florin (1931) arranged the species into three sections, A, B, and C, on the basis of their leaf epidermal structures. Florin himself stressed the provisional nature of these groupings, and pointed out that Section C, in particular, was clearly artificial. Subsequent studies by Quinn (1965, 1966a, 1966b) and Tengner (1965) indicate that the actual situation is far more complex.

Podocarpus, on the other hand, presents a much more clearly defined picture, as a result of the intensive studies of leaf anatomy made by Buchholz and Gray (1948). In this revision the genus was divided into eight sections, of which three, viz. *Eupodocarpus*, *Stachycarpus* and *Nageia*, were further subdivided into subsections.

While there has been a general acceptance of the smaller genera, there has developed a tendency to question the validity of these two large genera, *Podocarpus* and *Dacrydium* (e.g. Hair, 1963). The aim of this paper is to examine the validity of these genera as founded on presently accepted criteria, and to suggest a possible alternative treatment more in line with recent evidence.

CRITERIA OF PRESENT GENERIC BOUNDARIES

Present generic boundaries within the family are largely based on the structure of the female cone (see Table 1). There is convincing evidence that during the evolution of the Podocarpaceae the female cone has undergone increasing reduction in the number of fertile bracts (Florin, 1951: p. 363). Thus a cone containing only one or two fertile bracts, such as is found in some members of *Podocarpus* and *Dacrydium*, and in *Acmopyle*, is a specialized feature. Those genera which retain a recognizable cone with many fertile bracts, viz. *Saxegothaea* and *Microcachrys*, are primitive in this respect.

TABLE I
Morphology of the female cone and karyotypes in the Podocarpaceae

	Number of species	Number of fertile scales/cone	Position of cones	Orientation of ovules	Oviferous scale fused to	Karyotype*	
						n	Number of arms
PODOCARPUS							
<i>Afrocarpus</i>	6	1-2	axillary	inverted	integument	12	20
<i>Dacrycarpus</i>	10	1-2	terminal	inverted	bract and integument	10	20
<i>Eupodocarpus</i>	74	1-3	axillary	inverted	integument	17-20	19, 20
<i>Microcarpus</i>	1	1-2	terminal	inverted	integument	18	20
<i>Nageia</i>	7	1-2	axillary	inverted	integument	10, 13	20
<i>Polypodiopsis</i>	5	1-2	axillary†	inverted	integument	10	20
<i>Stachycarpus</i>	10	1-8	axillary	inverted	integument	18, 19	20
<i>Sundacarpus</i>	1	1-2	axillary	inverted	integument	19	20
DACRYDIUM							
Section A	3	1-2	terminal	semi-erect	(free)	10	20
Section B	13	1-5	terminal	semi-erect	(free)	10	20
Section C							
<i>D. bidwillii</i> group	3	1-3	terminal	inverted	(free)	9, 11, 12	16
<i>D. latifolium</i> group	2	1-2	terminal	erect	(free)	15	20
<i>D. colensoi</i> group	3	2-5	terminal	semi-erect	(free)	10, 15	20
ACMOPYLE	3	1-2	axillary†	semi-erect	integument	10	20
SAXEGOTHAEA	1	4-12	axillary	inverted	(free)	12	20
MICROCACHYRS	1	20-28	terminal	inverted	(free)	15	20
MICROSTROBOS	2	4-5	terminal	erect	(absent)	13	20
PHYLLOCLADUS	7	2-20	axillary	erect	(absent)	9	18

* Hair (1963) and Hair (pers. com.).

† sometimes terminal (de Laubenfels, pers. com.).

An epimatium or ovuliferous scale (or more correctly, the sterile part of the seed-scale complex—Florin, 1951: p. 364) is present in all the genera except *Phyllocladus* and *Microstrobos*. Both these genera have few species, and *Phyllocladus* is highly specialized in both karyotype (Table 1) and vegetative morphology. The presence of an ovuliferous scale in all but a few species, some of which were highly specialized in other respects, is consistent with the view that the ovuliferous scale is a primitive feature in the family, and that its absence in *Phyllocladus* and *Microstrobos* is due to reduction. Such an interpretation is also in line with Florin's theory of the origin of the coniferous cone, in which the ovuliferous scale is regarded as a primitive feature in the conifers as a whole (Florin, 1951).

Fusion between the ovuliferous scale and the integument is found throughout all sections of *Podocarpus* and in the genus *Acropyle*. While this occurrence could equally well fit either a primitive or derived feature, the fusion of two adjacent structures is more easily visualized than their separation from a single structure. Again, the fossil evidence indicates that such fusion is a derived feature for the conifers generally (Florin, 1951). It seems highly probable, therefore, that fusion of the ovuliferous scale with the integument is a specialization within this family.

Florin (1951) regards the erect ovule as primitive in the conifers as a whole, though the inverted condition was developed at a very early stage in the evolution of some lines. In the Podocarpaceae there is a complete range in ovule orientation from the erect type seen in *Microstrobos* and *Dacrydium laxifolium*, through intermediate types where the ovule is partly reflexed as in *D. cupressinum*, to the completely inverted ovule of *Podocarpus* and *Dacrydium bidwillii*. The fact that in *D. colensoi* the ovule becomes more erect during its development has been interpreted as an indication that some species have developed the erect condition secondarily (Sinnott, 1913). Inverted ovules characterise the Pinaceae (s. str.) and Araucariaceae, and are found along with erect ovules in the Taxodiaceae and Podocarpaceae. Thus a change in the orientation of the ovule has occurred several times in the evolution of the Coniferales. It is possible, therefore, that changes in either direction may have occurred more than once in the Podocarpaceae. Clearly, ovule orientation is a character to be used with caution in assessing affinities.

The terminal position of the female cones seen in *Dacrydium*, *Microcachrys*, *Microstrobos* and Sections *Dacrycarpus* and *Microcarpus* of *Podocarpus* is considered primitive, the axillary fertile shoots found elsewhere in the family having been derived from it.

The genus *Dacrydium* is at present constituted by species with relatively few fertile bracts in the female cone (1-6), the cones terminal on vegetative branches, and the ovuliferous scale present and free from the integument. Of these features, only the reduced cone is considered derived, and this is a specialization that has found very general expression in the family. The other features of cone morphology that serve to unite the genus, viz., the free ovuliferous scale and the terminal position of the cones, are both primitive conditions, and so do not indicate any close relationship between the species concerned. In other aspects of cone morphology there is considerable diversity. This is particularly evident in the orientation of the ovule, the size of the cone, and the development of the ovuliferous scale. There seems little support, then, for the retention of this genus on the basis of cone morphology alone.

All sections of *Podocarpus* show an inverted ovule with fusion between the ovuliferous scale and the integument, and a relatively reduced female cone (1-2 fertile bracts in all except *Stachycarpus*). It is the fusion between

the ovuliferous scale and the integument of the ovule that alone distinguishes all members of the genus from all those of *Dacrydium*. While such fusion is most probably a specialization, a development of this kind could easily have occurred more than once. In fact, it appears to have occurred at least twice in the family, being found in a somewhat different form in *Acropyle*, where it is associated with an erect ovule. Thus the retention of a genus defined by this character alone is hard to justify without strong supporting evidence.

It seems essential, therefore, that the present taxonomic boundaries of *Podocarpus* and *Dacrydium* should be critically evaluated in the light of more recent data drawn from the fields of cytology, embryology and anatomy.

CYTOLOGY

The karyotype of representatives of every genus and section in the family is now known (Hair, 1963). There is a range in chromosome number from $n = 9$ to $n = 20$ (Hair, pers. com.). Hair and Beuzenberg (1958) have established, however, that the number of major chromosome arms in the haploid complement is constant at 20 for all members of the family, with the notable exceptions of *Phyllocladus* (18), the *Dacrydium bidwillii* group of *Dacrydium* (16), and Subsections B and F of *Podocarpus* Section *Eupodocarpus* (19) (see Table 1). Many sections of *Podocarpus* show a high degree of uniformity in both the number and morphology of their chromosomes, which lends support to the groupings of these species made by Buchholz and Gray (1948). In *Dacrydium*, the karyotype has been established as $n = 10$, with 20 major arms, for all members of Sections A and B so far examined. There is wide variation in Section C, however, both in the number of chromosomes and major arms. This underlines the need for a revision of this section mentioned above.

While karyotype can be used to characterize several sections of *Podocarpus* and *Dacrydium* (see Hair, 1963), there are no features that set all members of either genus apart from the rest of the family. Indeed, the cytological differences between sections of the one genus are generally at least as great as those that separate the smaller genera of the family from one another.

GAMETOPHYTES AND EMBRYOGENY

Detailed accounts of gametophyte development and embryogeny are now available for representatives of every genus in the family except *Acropyle*, and for five of the eight sections of *Podocarpus*, as well as four of the species groups in *Dacrydium* (see Table 2). In most cases these details are available for only a single species. In some instances, however, observations have been made on two or more species. In the large and rather diverse *Eupodocarpus* records are available for at least some stages in *Podocarpus macrophyllus*, *P. coriaceus*, *P. glomeratus*, *P. latifolius*, *P. purdeanus*, *P. urbanii* and *P. totara*, which are drawn from three different subsections (B, C and D). These observations have been critically reviewed by Doyle in his thorough account of *P. nivalis* (Boyle and Doyle, 1953, 1954; Doyle, 1954). Also limited observations have been made on the male and female gametophytes and embryos of *P. ferrugineus* and *P. spicatus* (*Stachycarpus*; Sinnott, 1913), the female gametophyte of *P. imbricatus* (*Dacrycarpus*; Gibbs, 1912), the embryo of *P. usumbarensis* (*Afrocarpus*; Buchholz, 1941), the male and female gametophytes of *Dacrydium biforme* (*D. bidwillii* group; Sahni and Mitra, 1927), and the female gametophyte and embryo of *Phyllocladus glaucus* (Holloway, 1937). In each instance a high degree of uniformity is apparent within the genus, section or species group.

All species so far examined are characterized by a three-tiered proembryo with binucleate embryo initials. Furthermore, these initials always pass through a distinctive "embryo-tetrad" stage, as was first fully described by Looby and Doyle (1944). This pattern of embryogeny is unique to the Podocarpaceae, and its presence in all members investigated strongly supports the naturalness (phylogenetic unity) of the family.

Analysis of the data has led to the recognition of a primitive condition for the family in a number of features of the life cycle (Quinn, 1966*b*). The occurrence of these primitive conditions throughout the family was summarized in tabular form in the paper cited, and is reproduced here, with corrections and some modification, as Table 2. The point to be made is that each section of *Podocarpus* and *Dacrydium*, as well as each of the other four genera, appears to be characterized by a unique set of both primitive and advanced features, as would be expected if each represented the end of an independent line that has evolved from an ancestral stock common to the entire family. The variation that occurs in the number of embryo initials in the proembryo serves to illustrate the general pattern of evolution. It seems most probable that the primitive embryo possessed a large number of initials, and that there has been a tendency for reduction in their number. This tendency has been expressed to varying degrees in *Microstrobos*, *Microcaechrys*, *Dacrydium* Section B and *Podocarpus* Sections *Dacrycarpus* and *Afrocarpus*, reaching its fullest expression in Section *Eupodocarpus*, where the number of initials is generally only one to three. In some cases this reduction in embryo initials has been accompanied by a reduction in the number of cells in the proembryo as a whole (e.g. *Eupodocarpus*) while in other cases it has not (e.g. *Afrocarpus*). Thus, there has been a tendency for the primitive condition to become modified in certain ways, and those modifications have occurred independently, and to varying degrees, during the evolution of several different groups. A similar situation exists in the cytological evolution of the family (Hair and Beuzenberg, 1958).

The five sections of *Podocarpus* which have been studied do not have a single derived feature in common (see Table 2). The same is true for *Dacrydium*, with the possible exception of the differentiation of the two male gamete nuclei. There is, therefore, no evidence to support the grouping of these species into *Podocarpus* and *Dacrydium* as currently defined. The level of difference in gametophyte and embryological characters between the various sections of each of these genera is no less significant than the differences that separate the remaining genera in the family. In fact, *Podocarpus* includes a greater range of variation in these features than is found in all the rest of the family (cf. *Stachycarpus* and *Eupodocarpus*). The evidence of gametophyte and embryological studies therefore suggests that each section of *Podocarpus* and each of the species groups in *Dacrydium* is sufficiently distinct from all the rest of the family to be treated as a separate genus.

VEGETATIVE ANATOMY

Buchholz and Gray (1948) in the introduction to their revision of *Podocarpus*, stated that there was no evidence of a closer relationship between any of the eight sections of the genus that would justify their grouping into subgenera. It was their opinion that the genus consisted of eight equivalent groups which might be either subgenera or sections. A most comprehensive survey of the vegetative anatomy of the entire family has recently been undertaken by Tengner (1965, 1967). His studies of both leaf and wood anatomy have already demonstrated the heterogeneous nature of both *Podocarpus* and *Dacrydium*.

CONCLUSIONS

On the evidence presented above it is clear that both *Podocarpus* and *Dacrydium* represent artificial assemblages. It seems desirable that all the sections of *Podocarpus* should be raised to generic rank in order to reflect accurately their affinities within the family. Tengner (1965) has already demonstrated the need to divide *Dacrydium* into at least two separate genera, one containing Sections A and B as defined by Florin (1931), and the other Section C. On the basis of cytology, cone morphology and embryology, however, a further division of this last group into at least three genera seems essential. The first of these genera would comprise *Dacrydium laxifolium* and *Dacrydium intermedium*. The second would comprise *D. bidwillii*, *D. biforme* and *D. kirkii*. Each of these proposed genera shows a remarkable degree of cytological and morphological uniformity.

The three remaining species, *D. colensoi*, *D. franklinii* and *D. fonkii* show some similarity in cone morphology. However, Tengner (1965) has shown that they differ in several aspects of vegetative anatomy. Thus, a conclusion as to whether these three species form a closely related group and so constitute a single genus must await the results of more detailed studies.

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